

25. On the Origin of Flight in Birds.

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(Text-figures 1-7.)

In 1907 I brought forward the idea that birds originated from bipedal Dinosaur-like running reptiles in which the anterior extremities, on account of flapping movements, had gradually turned to wings without thereby affecting terrestrial locomotion (14). This idea has been on several occasions criticised by various authors (1, 3, 9, 12, 16).

In consequence of new material having turned up that has some bearing on this subject, the time seems to have arrived when the different criticisms to which the hypothesis of a "running *Proavis*" has been subjected can be reviewed.

The first criticism was brought forward by Hay (9), who disagreed with my idea on account of my having drawn *Proavis* with too short arms and with a reduced and rotated hallux. According to Hay's view, birds never could have originated from such a form unless considerable rejuvenation might be presumed. The Dinosaurs Hay supposes to have been originally quadrupedal.

Hay's view was endorsed by Abel (1), who, on account of the rotation of the hallux and the development of a prehensile manus in *Archaeopteryx* and Dinosaurs, in 1912 supported the idea that both birds and Dinosaurs were derived from arboreal forms. Steiner tried to derive arguments against my hypothesis from the diastaxic arrangement of the feathers, the origin of which he traced back to some arboreal Agamid (16). In a later paper (17) he likewise emphasised the prehensile structure of the manus in primitive birds, but at the same time he believed that Abel's arguments, based on hallux and pollex, were devoid of foundation.

Beebe (3) and Lucas (12) fully appreciate the difficulty that arises from the fact that, while in all arboricolous passive fliers the centre of the parachute surface coincides, as it must, with the centre of gravity of the animal, this could not have been the case in a primitive arboricolous bird having feathers only on its tail and arms. They think to overcome this difficulty by assuming that the most primitive arboreal birds had quills also on their legs.

This stage in avian evolution Beebe terms the *Tetrapteryx* stage; and in support of his hypothesis, he falls back on the observation that temporarily quills develop on the legs of several kinds of birds, and are later replaced by down.

In 1922 Abel (2) dropped the idea that birds and Dinosaurs originated from quadrupedal arboreal forms, and suggested that birds might be the offspring of a bipedal *Tarsius*-shaped reptile. Heilman tried (11) to reconcile my views with those held by Hay and Abel, etc.

It is apparent from this review, that anatomical arguments against the hypothesis of a running *Proavis* are mainly based on the structure of the manus and the pes, and partly on the occurrence of certain quills. None of the authors cited has considered either the shoulder-girdle or the pelvis of birds, in spite of these parts being correlated with the feet.

Since Hay and Abel's argument from the occurrence of a functional hallux in different birds is of great anatomical weight, it has to be dealt with first. The functional hallux in many birds must either be an old structure inherited from an arboreal *Proavis*, or it must be a newly-acquired character that was missing in the running *Proavis*.

Although we know comparatively little about the Triassic bipedal reptiles among which the running *Proavis* might be looked for, nevertheless by the study of fossil footprints some points of the structure of the feet of bipedal Triassic reptiles can be elucidated (13). In my argument, four types of Triassic footprints are of special interest, for they throw some light on the evolution of the hallux in these otherwise nearly unknown types. These four types can be grouped around the footprints called *Plectoterna*, *Ammopus*, *Anchisauripes*, and *Gigandipus*. Believing that I have proved all Dinosaurs to have developed from bipedal lightly-built animals (15), I consider these tracks to be Dinosaurian.

Plectoterna has long and slender toes, and a very long metatarsus resting always on the ground and indicating a plantigrade animal like *Hallopus* (text-fig. 1). *Ammopus* has also slender toes, but it shows, instead of the metatarsal impression only, the impression of a rounded pad, proving that this animal was digitigrade, as is *Procompsognathus* (text-fig. 2). *Anchisauripes* has thicker toes than either of these two types, and was frequently plantigrade. It is the track of *Anchisaurus* (10) (text-fig. 3). *Gigandipus* is of still heavier build, but always digitigrade, and the track of some unknown Megalosaurian.

Around each of these four types several other Triassic footprints can be grouped that differ mainly in the development of the hallux. To the *Plectoterna* type belong *Palamopus*, *Exocampe*, *Herpedactylus*, *Xiphopeza*, and *Corripes*; to the *Ammopus* type are allied *Eupalamopus*, *Polemarchus*, and *Platypterna*; the *Anchisauripes* type is suggested by *Anomæpus*, *Apatichnus*, and *Grallator*; and the *Gigandipus* type is approached by *Sauropus* and *Hyphepus*.

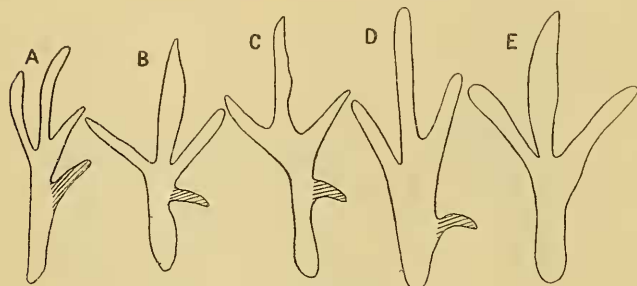
Considering the hallux of these different tracks, it may be remarked that in some the hallux articulates very low down and is not rotated (*Palamopus*, *Exocampe*, *Anomæpus*); in others the

rotation is more or less marked, but the hallux is still always well in touch with the ground (*Herpedactylus*, *Xiphopeza*, *Platypterna*, *Palamopus*, *Polemarchus*); yet in other tracks (*Ammopus*, *Apatichnus*, *Anchisauripus*, *Sauropus*) the rotation is still more accentuated, and the articulation is well raised above the ground, so that only the tip of the hallux makes an impression; and finally in some of the tracks (*Corvipes*, *Platypterna*, *Grallator*) the hallux can be seen no more.

Thus in all four types of tracks a simultaneous and independently acquired rotation and abbreviation of the hallux can be detected. Since it is quite impossible to assume that all four types of tracks were exclusively made by animals becoming arboreal, it is evident that the curious rotation of the hallux in all these types was not due to arboreal adaptation, but to some other hitherto unknown factor*.

The hallux that is attained in all these types recalls that

Text-figure 1.



Footprints of plantigrade Triassic reptiles.

(A) *Herpedactylus*; (B) *Xiphopeza*; (C) *Plectopterna*; (D) *Plectopterna*;
(E) *Corvipes*.

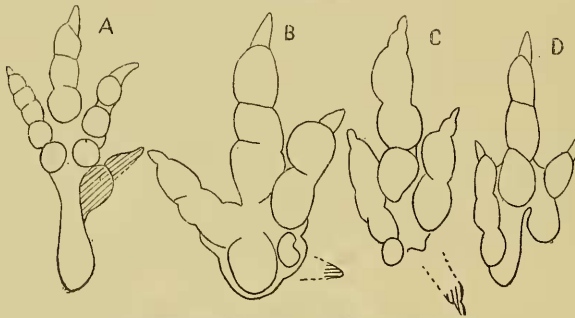
of those birds in which it is a non-functioning digit. If it can be proved that the functioning hallux in birds developed from a non-functioning hallux, this observation is a strong argument for a Dinosaur-like terrestrial bipedal running *Proavis*.

If the functioning hallux in birds developed from a non-functioning but rotated and abbreviated hallux, this change must have left some traces. In the functioning hallux of birds two distinct features seem actually to point to such a change. First, one may mention that even in birds with a strong functioning hallux the first metatarsal is reduced. This shows that in the history of these birds some stage of evolution was passed in which the hallux was but feebly attached to the leg, and when consequently the hallux was not much used for grasping.

* The reason why the rotated hallux is more reduced in some Dinosaurs than in others will be discussed on another occasion.

As a second feature pointing in the same direction, the great variety of the flexor muscles of the hallux can be brought forward. If the functioning type of hallux were the primitive type in birds, then the arrangement of the flexor muscles could be everywhere alike, whereas, if the hallux was rejuvenated and secondarily but independently strengthened in different groups of birds, the flexor muscles might vary. As is known, the latter is actually the case, and the variation has been used in the classification of birds (7). These detailed observations show that the functioning hallux in birds is perhaps a secondary adaptation. A feature worth mentioning is that in the apparently tridactyle foot of those bipedal animals that passed through a stage of arboreal specialisation (Kangaroo) the fourth toe is the longest (5), while it is the third that is the longest in Dinosaurs, birds, and *Alactaga* (14).

Text-figure 2.



Footprints of digitigrade Triassic reptiles.

(A) *Anomœpus*; (B) *Apatichnus*; (C) *Anchisauripus*; (D) *Grallator*.

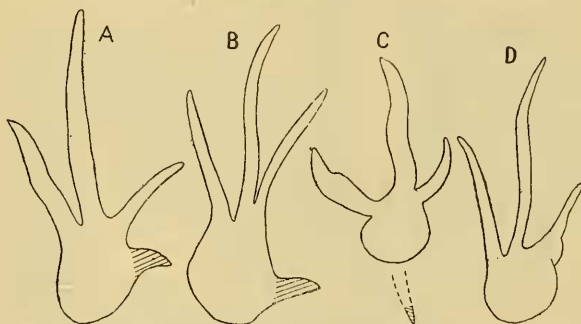
Turning now from the pes to the manus in primitive birds (*Archæopteryx*), it may be remarked that this is a long and slender organ, adapted to some extent for grasping, but this alone is again no sign of arboreal specialisation.

The partial use of the anterior limb as a grasping organ occurs in different terrestrial quadrupeds. The fore leg is used as a manus in the Kangaroo when taking up food; it is similarly used in mice and rabbits and, partly for the same purpose and partly also as a weapon, in cats and bears. Members of each of these groups are, it is true, partly also arboreal; but nevertheless the terrestrial representatives in these groups do not descend from the arboreal forms, for, on the contrary, it was the use of the anterior limb as a grasping organ that enabled some of the terrestrial forms to climb trees.

Steiner has proved in a recent highly valuable contribution (17)

that in most *Archosauria* the ulnar phalanges are reduced, while the radial phalanges are retained or sometimes even strengthened. He takes this to be a sign of the arboreal adaptation of *Proavis*. The reduction cannot be denied, but again it does not seem to be a sign of any arboreal specialisation. In the one group of extinct reptiles that certainly was derived from arboreal types this reduction does not take place, for in Pterosaurians the last finger is very strong, and this reduction does not occur in any of the arboreal mammals (5). It is well marked only in Crocodilia, Dinosaurs, and birds. The primitive Dinosaurs are, as is well known, bipedal (15). In the Crocodilia the reduction of the shoulder-girdle and the curious elongation of the carpal bones indicate that formerly also in this group the disproportion between the fore limbs and the hind limbs was also decidedly greater (10). Considering that all those mammals that are partly bipedal use the anterior limb for

Text-figure 3.



Footprints of digitigrade Triassic reptiles.

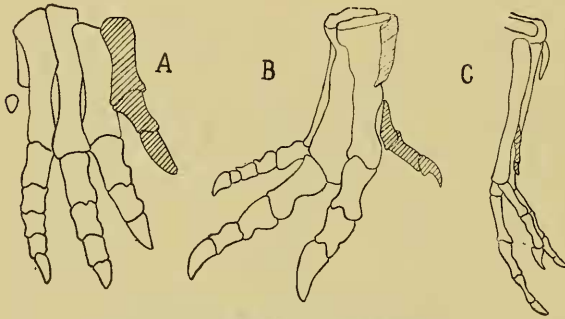
- (A) *Eupalamopus* (somewhat modified); (B) *Polemarchus*; (C) *Ammopus*;
(D) *Platypterna*.

grasping, and that Dinosaurs and Crocodilia are terrestrial forms with a strong posterior body, it should be investigated whether the ulnar reduction is not due to the use of the manus as a grasping organ during terrestrial and not during arboreal life. The first change that is attained when both the as yet unmodified anterior limbs are used together as a primitive grasping organ, is the inward rotation of both palmar surfaces; the next change that must be expected is a strengthening of the radial side, for in two palms that are half-way rotated the radial borders of the hands come always nearer together than the ulnar borders; consequently they are always exposed to much greater strain than the ulnar sides of the hands. This greater strain will be especially felt when the food is held with both anterior feet and pieces are detached with the teeth. Such a manus must of course differ strongly from the manus of every arboreal type, for in the

arboreal types it is of importance that the grasping surface of the whole hand should be as great as possible. This is attained by the retention of all phalanges, and especially by the retention of the fourth (5). In animals in which the function of the manus is different, a reduction of the ulnar phalanges, recalling somewhat the reduction of the fourth and fifth digits of the human hand, can take place.

The most reduced manus of this sort attained by a terrestrial animal is the manus of *Struthiomimus*, and the resemblance to the manus in *Archæopteryx* is quite easily made out (18). *Struthiomimus*, however, did not live on trees (text-fig. 5). This genus is not only suitable for demonstrating that a hand can be developed on *terra firma*, but also that a secondary elongation of the fore limb can be attained without adaptation to flight (18). Comparing the Triassic *Procompsognathus*, the Jurassic *Ornitholestes*, and the Cretaceous *Struthiomimus*, none of which were arboreal,

Text-figure 4.



Bones of pes in Dinosaurs.

(A) *Massospondylus*; (B) *Antrodromus*; (C) *Compsognathus*.

it may be remarked that the anterior limb is short in *Procompsognathus*, longer in *Ornitholestes*, and longest in *Struthiomimus*. This shows a steady increase in length. Since a similar elongation occurs also in the Sauropoda (for in this group the long-armed *Brachiosauridæ* certainly descended from the other, but short-armed forms) this elongation may well be compared with the elongation that can be seen in the anterior limb of the most primitive bird (*Archæopteryx*). It is a sort of rejuvenation that suggests also the rejuvenation of the avian hallux already discussed. This observation proves to a certain extent that Hay's objection to my drawing *Proavis* with relatively short arms does not weigh as much as it seems to do at first.

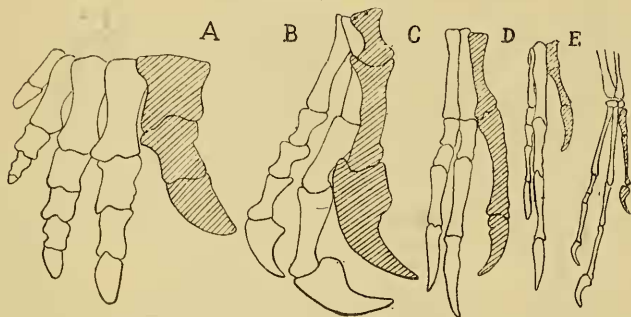
After having discovered in the course of our investigation that the similarity of hands and feet in birds and Dinosaurs, and their fundamental difference from these parts in all arboreal

mammals and lizards, not only do not form an argument for the arboreal origin of birds and Dinosaurs but on the contrary plead for their origin from running ancestors, and after having, as I believe, refuted the arguments brought forward by Abel, Hay, and Steiner, I think the next step should be to mention all those points in the anatomy of birds which exclude an arboreal *Proavis* from the history of this group.

All birds have a fused metatarsal. Where it is but feebly fused, as in the Penguins, this is a return to a primitive stage, for in the fossil Penguins of the Seymour Islands the metatarsals are more strongly fused than in any recent species (20).

With exception of arboreal birds, not a single arboreal vertebrate animal is known in which a fusion of the metatarsals is even indicated. This fusion shows that *Proavis* must have moved differently from all recent and fossil arboreal forms.

Text-figure 5.



Bones of manus in Dinosaurs and birds.

(A) *Massospondylus*; (B) *Antrodiesmus*; (C) *Struthiomimus*; (D) *Ornitholestes*;
(E) *Archaeopteryx*.

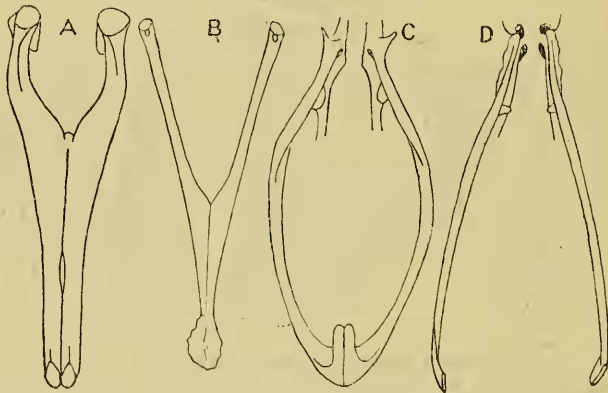
Proavis cannot have leaped in a more or less frog-like manner like *Tarsius*, *Galago*, or frogs, for in such arboreal animals the flexible tarsus is modified and its proximal part elongated; it cannot have climbed, for the manus is specialised on other lines; it cannot have jumped like a monkey, for birds show no tuber on the heel. Even *Pedetes*, though terrestrial and provided with compact tarsal bones, shows how even the firmly united tarsal bones are finally affected by jumping, for in the recent *Pedetes* these bones are somewhat elongated, while they are short in a more primitive fossil type that Prof. Stromer intends to describe. This elongation of the tarsal bones is necessary in jumping animals, for in these it is essential that that part of the pes should be rigid and long which immediately touches the tibia, and not the part beyond the flexible tarsal bones. In bipedal stalking and walking animals the metatarsals can more easily elongate so as to ensure a greater stride.

Since the fusion of the metatarsals occurs exclusively in terrestrial forms (*Alactaga*, etc., and *Artiodactyla*), *Proavis* must once have been terrestrial. Supposing *Proavis* acquired this marked specialisation while living in trees, it must have moved about there in a hitherto unknown fashion; supposing, however, that birds learnt to fly, and only then became bipedal, then we have a quite unique sort of evolution, for all those quadrupeds that learnt to fly in the quadrupedal state became unable to walk. Consequently birds must first have been bipedal, and only then have learnt to glide.

Another argument that can also be brought forward against the hypothesis of an arboreal *Proavis* can be deduced from the pelvis of the most primitive bird we know (*Archæopteryx*).

While the pes in *Archæopteryx* shows that this type had

Text-figure 6.



Pubes of Dinosaurs and birds.

(A) *Cælorus*; (B) *Archæopteryx*; (C) *Struthio*; (D) *Dromæus*.

already taken to arboreal life, the pelvis, as shown by the pubes, is of the long and narrow type. This type is only met with in Dinosaurs and one cursorial bird. In the other birds, and especially in the arboreal birds, the pelvis is usually broad and short, and the pubes are wide apart (text-fig. 6).

In accordance with this structure and with the abbreviation of the vertebral column, the arboreal birds mostly hop, while the ground-birds walk or run. In the best runners the body is the longest, and the pelvis always remarkably narrow. Since a long body and narrow pelvis are seen in *Archæopteryx* in a marked manner, its arboreal specialisation can only be called very slight. It was assuredly derived from a terrestrial stock.

The shoulder-girdle in birds also indicates that their common ancestor must have once passed through a terrestrial stage of

specialisation. Whenever in nearly-related Mammalia terrestrial and arboreal forms occur, it is in the latter that the clavicles are certainly present. According to Weber (19), the clavicles are missing in the terrestrial genus *Hystrix*, but present in the arboreal *Erethizon*.

Since in cursorial forms in which the humerus moves only in a plane that runs parallel to the body, no lateral strain is brought to bear on the glenoidal fossa, of course in such forms clavicles are useless, but they must be retained in the forms that extend the arms strongly sideways, for here such lateral strains occur.

If birds are derived from terrestrial forms in which the arms and the shoulder-girdle were temporarily reduced, it is in the shoulder-girdle that this must show.

In the Thecodontia, in which, as shown by the relative length of the fourth digit, the elbows stood yet somewhat off from the body, an interclavicle and clavicles are present; in the Crocodilia, only the interclavicle remains, but also the fourth toe is abbreviated, showing that the lateral strain on the leg was already relatively small; finally in all the Dinosaurs, as we know, clavicles and interclavicular are absent. In Dinosaurs, moreover, a well-ossified sternum is present, arising from two centres of ossification.

If we turn now from these reptiles to modern and extinct birds, we find always an osseous sternum and further on a bone that has been considered as corresponding to the clavicle of reptiles. This bone has been called the furcula, and it is this name that I adopt, for it has no phylogenetical meaning. In some birds this bone touches the sternum, in others, as *Archæopteryx*, it does not.

Not even the slightest trace of an interclavicle has ever been found in birds (6), although this bone has been eagerly sought for. The scapula and coracoid in *Archæopteryx* recall these elements in the primitive bipedal Dinosaurs and Struthious birds (text-fig. 7).

If the present arboreal birds are the direct descendants of a clavicle-bearing quadrupedal lizard-like reptile that took to climbing trees, surely a clavicle ought to be present, and perhaps even an interclavicle might be expected, for it is exactly the interclavicle that is retained both in Crocodiles and Mosasaurs when the osseous clavicles are already gone. If features exist that show that the furcula of birds is a newly-acquired bone and that both clavicles and interclavicle are gone, then this is an important argument in favour of a primitive running *Proavis*.

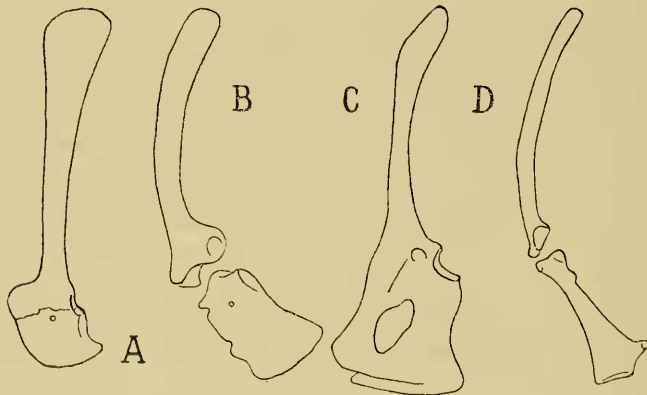
As can be seen, a great part of the question turns on the nature of the furcula of birds.

While the clavicles in all animals are always paired bones attached to the scapula with one end and to the interclavicle with the other, the furcula of birds adheres to the coracoid with one end and fuses, even in *Archæopteryx*, in the middle with the furcula from the other side.

If we wish to identify the furcula of birds with the clavicle of other vertebrata, we must assume that, first of all, the clavicle managed to slip along the anterior border of the scapula, then, to pass the glenoid fossa without, however, affecting the motion of the humerus by so doing, and finally to attach to the coracoid. Worse than that, we must also suppose that in the middle of the body a very curious, almost mysterious, and unique reduction managed to wipe out even the last ontogenetical trace of the interclavicle without affecting the clavicles. Surely it is somewhat risky to evoke a hypothesis of this sort.

Supposing now, instead of these changes, that the furcula is an ossified tendon that was developed when birds began to glide to strengthen a reduced scapular arch, it is easy to explain its origin on the coracoid, the primary fusion of the median ends, its

Text-figure 7.



Scapula and coracoid in Dinosaurs and birds.

(A) *Gorgosaurus*; (B) *Archaeopteryx*; (C) *Struthio*; (D) *Nothura*.

successive fixing on to the sternum, and the absence of clavicles and interclavicle. Of course it is necessary in this case to fall back on the hypothesis of a terrestrial and bipedal *Proavis* in which the shoulder-girdle had suffered reduction.

In accordance with some old zoologists, I consider the furcula to be an ossified tendon, and not to be homologous with the clavicles in reptiles. Since this supposition agrees with the results hitherto obtained, I think this hypothesis is the right one.

All evidence brought forward up to the present shows that the flying state of birds was preceded by a state of bipedal running. Having established this, of course it becomes necessary to investigate when and where primitive feathers and passive flight began.

If passive flight and feathers arose after cursorial reptiles had

taken up an arboreal life, they must have developed feathers on arms and legs, for also in these long-necked and long-tailed forms the centre of the supporting gliding surface had to coincide with the centre of gravity of the body. Hence, evidently out of these reptiles a *Tetrapteryx* had to develop.

Of course an exclusively bipedal *Tetrapteryx* would encounter great difficulties when climbing. During gliding, furthermore, in spite of new difficulties presenting themselves, the knees of such a creature had evidently to be turned outward; the feet had to be stretched away from the body and had to be brought into the same plane as the anterior members, else the feathers of the legs would have been quite ineffective. All this and the difficulties encountered when climbing without using the anterior limbs would have been very detrimental to bipedal locomotion. Even a mere glance at Beebe's hypothetical *Tetrapteryx* shows that such a creature could not have been bipedal.

Since Beebe's *Tetrapteryx* is a rather short-necked animal, this point of his drawing is likewise open to criticism. All birds originated evidently from a bipedal and long-necked ancestor that carried the head upright. It will, however, always remain an unsolved problem how *Tetrapteryx* could have managed to carry such a long neck and an upright head when gliding: arboreal animals are rather short-necked.

In consequence of all this, the *Tetrapteryx* hypothesis, which is but a revival of Pycraft's arboreal *Proavis*, must evidently be dismissed, for it can in no way account for the persistence of bipedal locomotion in birds.

The whole *Tetrapteryx* hypothesis is based exclusively on the one interesting observation, that in some birds a row of quills is present on the upper part of the legs.

Without diminishing the interest of this observation, it has to be remarked that in a long-tailed animal this is the very place where quills would be ineffective, and that the phylogenetical value of this observation varies according to the manner in which one estimates the relation between quills and down.

If the down is considered to be the primitive type of feather which originated as a body cover to prevent the loss of heat, and the quills are considered as its modification, of course in such a case the occurrence of a row of quills on the leg can be taken as a proof that the legs were once used for flying; but if, on the other hand, the quills are considered as primitive, then such a reasoning is fallacious. In this latter case the occurrence of quills in places that are later covered with down possibly only shows that formerly a part of the side of the body of the primitive birds was covered with quills arranged in rows. Such quills can then gradually have been replaced by down, except in places where they served for flight or steering.

In such a case it may be assumed that the quills which evidently first originated on the arms and tail gradually spread to adjacent places where they were not really wanted.

A hypothesis that assumes that organs that develop in one part should be capable of spreading on to adjacent regions where they are of little or no value, needs naturally to be proved.

In all species of Rhinoceroses in which a strong nasal rugosity is present to serve as base for the dermal horns, the surface of the jugal arch, the lacrymal, prefrontal, the otic region, and even the posterior and exterior surface of the mandible, is also rough (*Rh. sumatrensis*, *Rh. bicornis*). In those Rhinoceroses, however, in which the nasal tuberosity is weak or wanting, the jugal and lacrymal and the other bones mentioned above are also smooth (*Rh. unicornis*, *Aceratherium*).

A similar feature, as in *Rhinoceros*, can be found also in Suidæ. *Hylæochærus* does not only show strong rugosities on the maxillaries and jugals, where the facial warts are developed, but also on the mandible and the frontal. *Sus verrucosus* shows similar but less marked features. Contrary to this, in *Sus barbatus* and *Sus cristatus* all the skull bones are smooth, and correspondingly on the cheeks strong warts and rugosities are wanting.

That the rapidly spreading rugosities in *Rhinoceros* and *Sus*, though in connection with warts, do not exclusively depend on the presence of these excrescences, can be demonstrated by the different Giraffes. Also in the latter a spreading of exostosis is traceable until the whole head is covered and even the mandible is affected: nevertheless, the skin in these animals remains smooth, and is quite normally covered with hair. Less clearly than in these three groups, the spreading of useless exostosis can be observed in the bovine tribe. In *Bos bubalis*, *Bos gaurus*, and the Bison, all of which have strong bony horn-cores, the rugosities of the frontal spread to the orbital and otic region, while in *Bos depressicornis*, in which the horn-cores are weak, the orbital and otic region is smooth. Bearing all these facts in mind, and they could easily be multiplied, and considering furthermore that in Crocodiles the skull bones and the bones of the dermal armour are of altogether different origin but that they nevertheless show the same pattern of sculpture, and that thus also they show the spreading of one feature over the whole body and that something similar occurs in *Lepidosteus* (8), I think it is not too much to assume that also in the primitive *Proavis* the primitive feathers of the tail spread even to regions where they were not wanted. Their attachment on a patagium is the best proof that they never functioned. That the primitive feathers of birds were quills and not, as generally thought, down was recently proved by Steiner (17).

In this way also Beebe's chief argument for the reconstruction of his *Tetrapteryx* loses a great deal of its value. It only shows that first in birds only a marginal row of quills was developed on the arms and on the tail, that later these spread towards the feet, and that the rest of the quills spring up later.

Summing up, one can safely state that in the skeleton of recent

and extinct birds not a single character can be detected which points conclusively towards a primitive arboreal adaptation, but that several skeletal characters can only be explained by the hypothesis of a cursorial running ancestor of birds. The otherwise inexplicable features are: the fused median metatarsals, the reduction of the first metatarsus, the small tarsal bones, the position of the knee, the long symphysis of the pubes in *Archæopteryx*, the lack of clavicles and interclavicle in all birds, and the position of the occipital condyle. The latter is vertical in birds and primitive Dinosaurs, and proves that, unlike arboreal forms, in both these long-necked groups the head was primarily carried upright on a sigmoidal neck.

Apart from all these important points, it is only by means of the running-*Proavis* hypothesis that the early occurrence of numerous flightless birds can be explained. It is evident that badly flying ground birds will much more readily return to exclusively cursorial habits than arboreal birds, for these, before becoming again flightless, must first descend from their trees and become thoroughly adapted to ground life. There exists a great difference between the pelvis of formerly arboreal flightless birds (for example, Dodo) and that of the Palæognathæ.

The hypothesis of a running *Proavis* is also the single one that accounts for the primitive structure of the palate, the free dorsal vertebrae, the low body-temperature, and the strong penis of the greater part of the Palæognathæ, for according to this hypothesis these birds are, of course, much nearer related to *Proavis* than the later and evidently more specialised arboreal birds. If the birds were of arboreal origin, one would expect the most primitive birds among the arboreal and not the terrestrial birds. In compliance with a wish of Steiner (17), I desist from using in the course of these comparisons the term *Ratitæ*.

That in one primitive arboreal bird more specialised, however, than an ostrich (i. e. *Opisthocomus*) the claws of the wing are more used for climbing than in all the other recent birds, is not of very great weight, for other nestlings use even their beak when climbing, and yet nobody will consider the Parrots to be ancestral to all the other birds. The climbing of *Opisthocomus* may quite well be regarded as a secondary adaptation, for the development of the pinions of the wings in *Opisthocomus* suffers a curious retardation that points in this direction (14). The sternum of *Opisthocomus* shows likewise a curious modification.

The primitive structure of the nest of ground birds when compared with the nest of the arboreal birds, and the more brilliant coloration of the latter, also agree very well with the hypothesis of the terrestrial origin of all birds. Even the curious fact that the nestlings of ground birds as a rule leave their nest comparatively soon after birth seems to some extent to favour this hypothesis (14).

Up to the present all critics of the "running *Proavis*" hypothesis have only tried to find apparent difficulties in that hypothesis,

and have never considered what it explains; now it is their turn to explain all the points that have been brought forward in the course of this paper by means of their hypothesis of an arboreal *Proavis*. It may be that more difficulties will be encountered than are expected.

Some critics (12) say that the comparison of a running *Proavis* with the different flying fishes is no comparison at all, because fishes do not move their pectoral fins in flight. In spite of this, I repeat that the comparison is rather a good one because

- (a) both types are vertebrata in which the anterior limbs are primarily only used for a similar passive gliding;
- (b) in both, during gliding the centre of gravity is behind the upholding surface, giving it a convenient elevation;
- (c) in both types the motive power used on land or in water is situated at the posterior end of the body and behind the gliding-planes;
- (d) in both, the locomotive power can immediately be brought again into action as soon as gliding through the air ceases, and so gliding can soon be regained.

None of these four characters can be found in arboreal passive fliers.

Zschokke (21) has remarked that some Crustacea develop a sort of flying like that of flying fishes; so there is no reason why a terrestrial vertebrate animal should not also have been capable of developing it. No mechanical difficulties exist. To those who go on to argue that, with the exception of flying fishes, all other flying vertebrates descended from arboreal animals, and that therefore this was presumably also the case in birds, I retort that, with the exception of flying snakes, all arboreal vertebrata and naturally all their flying offspring are without exception quadrupedal, while this is not the case in birds.

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